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Arabidopsis TCH4, regulated by hormones and the environment, encodes a xyloglucan endotransglycosylase.

Xu W, Purugganan MM, Polisensky DH, Antosiewicz DM, Fry SC, Braam J.

Department of Biochemistry and Cell Biology, Rice University, Houston, Texas 77251-1892, USA.

Adaptation of plants to environmental conditions requires that sensing of external stimuli be linked to mechanisms of morphogenesis. The Arabidopsis TCH (for touch) genes are rapidly upregulated in expression in response to environmental stimuli, but a connection between this molecular response and developmental alterations has not been established. We identified TCH4 as a xyloglucan endotransglycosylase by sequence similarity and enzyme activity. Xyloglucan endotransglycosylases most likely modify cell walls, a fundamental determinant of plant form. We determined that TCH4 expression is regulated by auxin and brassinosteroids, by environmental stimuli, and during development, by a 1-kb region. Expression was restricted to expanding tissues and organs that undergo cell wall modification. Regulation of genes encoding cell wall-modifying enzymes, such as TCH4, may underlie plant morphogenetic responses to the environment.

PMID: 7580251 [PubMed - indexed for MEDLINE]

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ACL5: an *Arabidopsis* gene required for internodal elongation after flowering.

Hanzawa Y, Takahashi T, Komeda Y.

Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo, Japan.

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In rosette plants, the formation of initial flowers is closely linked to the lengthening of internodes (bolting). In order to clarify the molecular basis of bolting, mutants with reduced lengths of internodes were screened. This paper presents the identification and characterization of recessive mutations in ACAULIS5 (ACL5), a gene required for internodal growth in *Arabidopsis thaliana*. Unlike previously described mutants with reduced size of organs, the acl5 mutant has a severe defect that is restricted to the process of cell elongation after transition to the reproductive stage and shows no phenotype before floral induction. The results of RNA blot hybridizations showed that the acl5 mutation causes a striking reduction in the transcript levels of genes encoding the tonoplast intrinsic protein (gamma-TIP) and the endoxyloglucan transferase (EXGT-A1), both of which have recently been suggested to be important for cell elongation. Furthermore, our morphological study indicates that the mutation also causes proliferative arrest of the apical inflorescence meristem. These results strongly suggest that, during the reproductive phase, the wild-type ACL5 gene product has a critical function not only in the control of elongation growth of organs but also in the continued maintenance of the proliferative activity of flower-producing meristems.

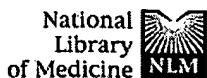
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Expression of endoxyloglucan transferase genes in acaulis mutants of *Arabidopsis*.

Akamatsu T, Hanzawa Y, Ohtake Y, Takahashi T, Nishitani K, Komeda Y.

Division of Biological Sciences, Graduate School of Science, Hokkaido University, N10, W8, Sapporo 060-0810, Japan.

A mutant of *Arabidopsis* with reduced internodal cell length, *acaulis5* (*acl5*), has recently been shown to have reduced transcript levels of a gene for endoxyloglucan transferase, EXGT-A1 (Y. Hanzawa, T. Takahashi, Y. Komeda [1997] *Plant J* 12: 863-874). In the present study, we cloned genomic fragments of five members of the EXGT gene family, EXGT-A1, EXGT-A3, EXGT-A4, XTR2, and XTR3, and examined their expression in the wild type and in a series of *acl* mutants. In wild-type plants, the EXGT-A3 gene showed higher expression in lower internodes (internodes between nodes bearing axillary shoots) than in upper and young internodes, in which EXGT-A1 was highly expressed. EXGT-A4 was preferentially expressed in roots and XTR3 in siliques. The XTR2 gene was constitutively expressed. In *acl1*, *acl3*, and *acl4* mutants, which have a severe defect in leaf expansion as well as in internode elongation, the EXGT-A1 gene showed reduced levels of expression before bolting of plants. In contrast, XTR3 was increased in these mutant seedlings. Reduction of EXGT-A1 expression was also detected after bolting of all *acl* mutants except *acl2*, whose growth defect is restricted to lower internodes. These results suggest the involvement of each EXGT in different aspects of organ development.

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Molecular characterization of a xyloglucan-specific endo-(1-->4)-beta-D-glucanase (xyloglucan endo-transglycosylase) from nasturtium seeds.

de Silva J, Jarman CD, Arrowsmith DA, Stronach MS, Chengappa S, Sidebottom C, Reid JS.

Colworth Laboratory, Sharnbrook, Bedford, UK.

A novel xyloglucan-specific endo-(1-->4)-beta-D-glucanase, involved in the post-germinative mobilization of xyloglucan storage reserves, has previously been isolated from nasturtium (*Tropaeolum majus* L.) seed. Its mode of action has been shown, *in vitro*, to be one of transglycosylation except at low substrate (glycosylacceptor) concentrations when hydrolysis predominates. Here it is shown that this nasturtium seed xyloglucan endo-transglycosylase is encoded by a single gene which is transcribed and processed to a 1.5 kb mRNA. The isolation and DNA sequence analysis of a cDNA copy of the nasturtium xyloglucan endo-transglycosylase transcript is described. The cDNA encodes a 33.5 kDa precursor polypeptide which is subsequently processed to a 31 kDa mature protein. The precursor incorporates an N-terminal signal sequence which probably contains information relevant to the targeting of the enzyme to the cell wall. The computer-predicted isoelectric point (5.14) and low (approximately 0%) alpha-helix content of the deduced mature protein are in excellent agreement with the experimental data obtained using the purified enzyme. The deduced protein sequence lacks homology with known plant endo-(1-->4)-beta-D-glucanases, consistent with the unique properties of the enzyme. Database searches have revealed that a *Brassica* protein (meri-5) of previously unknown function, but abundantly expressed in expanding tissue, shares structural identity with the nasturtium xyloglucan endo-transglycosylase. The expression of a xyloglucan endo-transglycosylase in expanding tissue would be consistent with the contention that enzymes of this type are involved in cell wall loosening.

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Xyloglucan endotransglycosylase, a new wall-loosening enzyme activity from plants.

Fry SC, Smith RC, Renwick KF, Martin DJ, Hodge SK, Matthews KJ.

Division of Biological Sciences, University of Edinburgh, U.K.

1. Cell-free extracts of all plants tested contained a novel enzyme activity (xyloglucan endotransglycosylase, XET) able to transfer a high-Mr portion from a donor xyloglucan to a suitable acceptor such as a xyloglucan-derived nonasaccharide (Glc4Xyl3GalFuc; XG9). 2. A simple assay for the enzyme, using [³H]XG9 and based on the ability of the [³H]polysaccharide product to bind to filter paper, is described. 3. The enzyme was highly specific for xyloglucan as the glycosyl donor, and showed negligible transglycosylation of other polysaccharides, including CM-cellulose. 4. The Km for XG9 was 50 microM; certain other ³H-labelled xyloglucan oligosaccharides also acted as acceptors, and certain non-radioactive xyloglucan oligosaccharides competed with [³H]XG9 as acceptor; the minimum acceptor structure was deduced to be: [formula: see text] 5. The pH optimum was approx. 5.5 and the enzyme was less than half as active at pH 7.0. The enzyme was slightly activated by Ca²⁺, Mg²⁺, Mn²⁺, spermidine, ascorbate and 2-mercaptoethanol, and inhibited by Ag⁺, Hg²⁺, Zn²⁺ and La³⁺. 6. XET activity was essentially completely extracted by aqueous solutions of low ionic strength; Triton X-100, Ca²⁺, La³⁺, and Li⁺ did not enhance extraction. Negligible activity was left in the unextractable (cell-wall-rich) residue. 7. The enzyme differed from the major cellulases (EC 3.2.1.4) of pea in: (a) susceptibility to inhibition by cello-oligosaccharides, (b) polysaccharide substrate specificity, (c) inducibility by auxin, (d) requirement for salt in the extraction buffer and (e) activation by 2-mercaptoethanol. XET is therefore concluded to be a new enzyme activity (xyloglucan: xyloglucan xyloglucantransferase; EC 2.4.1.-). 8. XET was detected in extracts of the growing portions of dicotyledons, monocotyledons (graminaceous and liliaceous) and bryophytes. 9. The activity was positively correlated with growth rate in different zones of the pea stem. 10. We propose that XET is responsible for cutting and rejoining intermicrofibrillar xyloglucan chains and that it thus causes the wall-loosening required for plant cell expansion.

PMID: 1554366 [PubMed - indexed for MEDLINE]



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Oligosaccharins--oligosaccharides that regulate growth, development and defence responses in plants.

Darvill A, Augur C, Bergmann C, Carlson RW, Cheong JJ, Eberhard S, Hahn MG, Lo VM, Marfa V, Meyer B, et al.

Complex Carbohydrate Research Center, University of Georgia, Athens 30602.

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The relationship between xyloglucan endotransglycosylase and in-vitro cell wall extension in cucumber hypocotyls.

McQueen-Mason SJ, Fry SC, Durachko DM, Cosgrove DJ.

Department of Biology, Pennsylvania State University, PA.

It has been proposed that cell wall loosening during plant cell growth may be mediated by the endotransglycosylation of load-bearing polymers, specifically of xyloglucans, within the cell wall. A xyloglucan endotransglycosylase (XET) with such activity has recently been identified in several plant species. Two cell wall proteins capable of inducing the extension of plant cell walls have also recently been identified in cucumber hypocotyls. In this report we examine three questions: (1) Does XET induce the extension of isolated cell walls? (2) Do the extension-inducing proteins possess XET activity? (3) Is the activity of the extension-inducing proteins modulated by a xyloglucan nonasaccharide (Glc4-Xyl3-Gal2)? We found that the soluble proteins from growing cucumber (*cucumis sativum L.*) hypocotyls contained high XET activity but did not induce wall extension. Highly purified wall-protein fractions from the same tissue had high extension-inducing activity but little or no XET activity. The XET activity was higher at pH 5.5 than at pH 4.5, while extension activity showed the opposite sensitivity to pH. Reconstituted wall extension was unaffected by the presence of a xyloglucan nonasaccharide (Glc4-Xyl3-Gal2), an oligosaccharide previously shown to accelerate growth in pea stems and hypothesized to facilitate growth through an effect on XET-induced cell wall loosening. We conclude that XET activity alone is neither sufficient nor necessary for extension of isolated walls from cucumber hypocotyls.

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Oligosaccharides as signals and substrates in the plant cell wall.

Fry SC, Aldington S, Hetherington PR, Aitken J.

Centre for Plant Science, University of Edinburgh, United Kingdom.

Publication Types:

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Cell wall carbohydrates as signals in plants.

Mohnen D, Hahn MG.

Complex Carbohydrate Research Center, University of Georgia, Athens
30602-4712.

Plant and fungal cells are surrounded by a cell wall rich in diverse polysaccharides and proteins. It has become apparent in recent years that the carbohydrates in the cell wall function not only to maintain cell shape and integrity, but also may serve as signals in plants. This review summarizes the evidence that biologically-active oligosaccharides (oligosaccharins) released from plant or microbial cell walls can serve as signals to regulate plant defense and plant growth and development. The oligosaccharins discussed include the fungal-derived hepta-beta-glucoside and the plant cell wall-derived oligogalacturonides and xyloglucans. Possible mechanisms by which oligosaccharins may exert their effects on plant cells are discussed.

Publication Types:

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Structure and expression of a barley acidic beta-glucanase gene.

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Monsanto Agricultural Group, New Products Division, St. Louis, MO 63198.

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A barley acidic beta-1,3-glucanase gene was recovered from a barley genomic library by homology with a partial cDNA of barley basic beta-1,3-glucanase isoenzyme GII. The gene, Abg2, is homologous to the PR2 family of pathogenesis-related beta-1,3-glucanase genes. The ABG2 protein has 81% amino acid similarity to barley basic beta-1,3-glucanase GII. The ABG2 protein is encoded as a preprotein of 336 amino acids including a 28 amino acid signal peptide. A 299 bp intron occurs within codon 25. The mature ABG2 protein has a predicted mass of 32,642 Da and a calculated isoelectric point of 4.9. The second exon of the Abg2 gene shows a strong preference for G + C in the third position of degenerate codons. The Abg2 gene was functionally expressed in Escherichia coli. Abg2 mRNA is constitutively expressed in barley root; leaf expression of Abg2 mRNA is induced by mercuric chloride and infection by Erysiphe graminis f. sp. hordei. Southern blot analysis indicates that Abg2 is a member of a small gene family.

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Regulated expression of the calmodulin-related TCH genes in cultured *Arabidopsis* cells: induction by calcium and heat shock.

Braam J.

Department of Biochemistry and Cell Biology, Rice University, Houston, TX 77251-1892.

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Expression of the calmodulin-related TCH genes of *Arabidopsis* is strongly and rapidly up-regulated in plants after a variety of stimuli, including touch. As an approach to investigating the mechanism(s) of TCH gene regulation, a manipulable cell culture system in which TCH gene expression is regulated has been developed. In response to increased external calcium or heat shock, TCH2, -3, and -4 mRNA levels significantly increased. Significantly, these two stimuli are known to result in cytoplasmic calcium increases, therefore implicating a role for calcium itself in the regulation of calmodulin-related genes. Further, external calcium is required for maximal heat-shock induction of expression of the TCH genes but not of the 70-kDa heat shock protein; therefore, there may exist at least two distinct mechanisms of heat shock induction of gene expression. Calcium ion regulation of genes encoding calcium-binding proteins may ensure the efficacy of calcium ion as a transient second messenger and the maintenance of cellular homeostasis. This possible regulatory circuit would likely be relevant not only for plant cells but also for the great variety of animal cells that transduce extracellular stimuli, such as hormones and electrical impulses, into calcium signals.

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Timing of events during flower organogenesis: *Arabidopsis* as a model system.

Lord EM, Crone W, Hill JP.

Department of Botany and Plant Sciences, University of California, Riverside 92521.

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Genetic analyses of signalling in flower development using Arabidopsis.

Okada K, Shimura Y.

Division 1 of Gene Expression and Regulation, National Institute for Basic Biology, Okazaki, Japan.

Flower development can be divided into four major steps: phase transition from vegetative to reproductive growth, formation of inflorescence meristem, formation and identity determination of floral organs, and growth and maturation of floral organs. Intercellular and intracellular signalling mechanisms must have important roles in each step of flower development, because it requires cell division, cell growth, and cell differentiation in a concerted fashion. Molecular genetic analysis of the process has started by isolation of a series of mutants with unusual flowering time, with aberrant structure in inflorescence and in flowers, and with no self-fertilization. At present more than 60 genes are identified from *Arabidopsis thaliana* and some of them have cloned. Although the information is still limited, several types of signalling systems are revealed. In this review, we summarize the present genetic aspects of the signalling network underlying the processes of flower development.

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Action of a pure xyloglucan endo-transglycosylase (formerly called xyloglucan-specific endo-(1-->4)-beta-D-glucanase) from the cotyledons of germinated nasturtium seeds.**Fanutti C, Gidley MJ, Reid JS.**

Department of Biological and Molecular Sciences, School of Natural Sciences, University of Stirling, UK.

The action on tamarind seed xyloglucan of the pure, xyloglucan-specific endo-(1-->4)-beta-D-glucanase from nasturtium (*Tropaeolum majus L.*) cotyledons has been compared with that of a pure endo-(1-->)-beta-D-glucanase ('cellulase') of fungal origin. The fungal enzyme hydrolysed the polysaccharide almost completely to a mixture of the four xyloglucan oligosaccharides: [formula: see text] Exhaustive digestion with the nasturtium enzyme gave the same four oligosaccharides plus large amounts of higher oligosaccharides and higher-polymeric material. Five of the product oligosaccharides (D, E, F, G, H) were purified and shown to be dimers of oligosaccharides A to C. D (glc8xyl6) had the structure A-->A, H (glc8xyl6 gal4) was C-->C, whereas E (glc8xyl6gal), F (glc8xyl6gal2) and G (glc8xyl6gal3) were mixtures of structural isomers with the appropriate composition. For example, F contained B2-->B2 (30%), A-->C (30%), C-->A (20%), B2-->B1 (15%) and others (about 5%). At moderate concentration (about 3 mM) oligosaccharides D to H were not further hydrolysed by the nasturtium enzyme, but underwent transglycosylation to give oligosaccharides from the group A, B, C, plus higher oligomeric structures. At lower substrate concentrations, hydrolysis was observed. Similarly, tamarind seed xyloglucan was hydrolysed to a greater extent at lower concentrations. It is concluded that the xyloglucan-specific nasturtium-seed endo-(1-->4)-beta-D-glucanase has a powerful xyloglucan-xyloglucan endo-transglycosylase activity in addition to its known xyloglucan-specific hydrolytic action. It would be more appropriately classified as a xyloglucan endo-transglycosylase. The action and specificity of the nasturtium enzyme are discussed in the context of xyloglucan metabolism in the cell walls of seeds and in other plant tissues.

PMID: 8374618 [PubMed - indexed for MEDLINE]



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Putative biological action of oligosaccharides on enzymes involved in cell-wall development.

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Joseleau JP, Chambat G, Cortelazzo A, Faik A, Ruel K.

Centre de Recherches sur les Macromolecules Végétales (CERMAV-CNRS),
Grenoble, France.

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Science 250, 948-954 1990.
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1: Plant Physiol 1996 Aug;111(4):1271-9

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Cold-shock regulation of the *Arabidopsis TCH* genes and the effects of modulating intracellular calcium levels.

Polisensky DH, Braam J.

Department of Biochemistry and Cell Biology, Rice University, Houston, Texas 77005-1892, USA.

The *Arabidopsis TCH* genes, which encode calmodulin-related proteins and a xyloglucan endotransglycosylase, are shown to be up-regulated in expression following cold shock. We investigated a possible role of fluctuations in intracellular calcium ion concentrations ($[Ca^{2+}]$) in the cold-shock-induced *TCH* gene expression. Transgenic plants harboring the *apoaequorin* gene were generated to monitor $[Ca^{2+}]$ and to test the necessity of cold-induced $[Ca^{2+}]$ increases for *TCH* expression. Cold-shock-induced $[Ca^{2+}]$ increases can be blocked by La³⁺ and Gd³⁺, putative plasma membrane Ca²⁺ channel blockers, and 1,2-bis(o-aminophenoxy)ethane-N,N,N',N'-tetraacetic acid, an extracellular Ca²⁺ chelator. Cold-shock-induced expression of the *TCH* genes is inhibited by levels of La³⁺, Gd³⁺, and 1,2-bis(o-aminophenoxy)ethane-N,N,N',N'-tetraacetic acid, that have been shown to block $[Ca^{2+}]$ increases. These data support the hypotheses that (a) intracellular $[Ca^{2+}]$ increases following cold shock require extracellular Ca²⁺ and may derive from a Ca²⁺ influx mediated by plasmalemma Ca²⁺ channels, and (b) cold up-regulation of expression of at least a subset of the *TCH* genes requires an intracellular $[Ca^{2+}]$ increase. The inhibitors are also shown to have stimulus-independent effects on gene expression, providing strong evidence that these commonly used chemicals have more complex effects than generally reported.

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